Reference: *Biol. Bull.*, **142**: 271–280. (April, 1972)

ON THE ENDOGENOUS CONTROL OF TIDE-ASSOCIATED DISPLACEMENTS OF PINK SHRIMP, *PENAEUS DUORARUM* BURKENROAD [1]

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Extensive movements are carried out by pink shrimp during the course of their life cycle. In the population studied here the larval and postlarval stages move, or are displaced, from their offshore spawning sites within the Gulf of Mexico to inshore nursery areas within the Florida Everglades. They remain within these inshore waters for several months, during which they undergo rapid growth, before returning again, as juveniles, to deeper offshore waters.

It is now well established (Tabb, Dubrow and Jones, 1962; Hughes, 1969c; Beardsley, 1970; Roessler and Rehrer, in press) that the inshore and offshore movements of the postlarvae and juveniles, respectively, are facilitated by the selective use of tidal currents. From the sampling of consecutive tides in a canal leading into the Everglades, the above mentioned workers found that postlarvae were taken predominantly in flood tide samples, whereas juveniles were taken exclusively during the ebbing tide.

An earlier study (Hughes, 1969a) indicated the probable mechanisms whereby postlarval and juvenile pink shrimp discriminate between and utilize the tides for their inshore and offshore displacements. It was shown that the shrimp were able to perceive and respond appropriately to very small changes of salinity, well within the range of salinity change normally occurring between tides in the vicinity of the everglades. Although these results suggest the probable mechanism whereby tide-associated movements take place in this species, they do not preclude the possibility that other aspects of water quality, which change with change in tide, could similarly elicit behavior changes, enabling the use of tides for displacements.

There is also evidence that the behavior responsible for these displacements is under endogenous control (Hughes, 1969b). Both the direction of swimming (with respect to the current) and the velocity of swimming of migrating juvenile pink shrimp within a current chamber, showed a phase relationship with the tide cycle in the area from which the shrimp had been collected the previous day. This relationship appeared to be adaptive in so far as downstream swimming was confined to the time of the ebb tide. (In nature, juvenile shrimp, migrating out of inshore waters, are found almost exclusively within the water column of ebbing tides.) It was concluded that some aspect of the tide cycle to which the shrimp were exposed prior to capture entrains a pattern of swimming which may persist for at least two days in a current, constant in terms of speed and "water quality."

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From these results the nature and extent of this control was not clear. This paper describes a subsequent study aimed at elucidating the role played by internal rhythms in the movements of both postlarval and juvenile pink shrimp.

Apparatus and Methods

Two identical current chambers were used in all experiments. These have been described before (Hughes, 1969a) and are modifications of the chambers used by Creutzberg (1961) in his study of tide-associated displacements of elvers. These chambers were maintained in a light-tight room, in which illumination was constant throughout all experiments and was provided only by single 10 w red bulbs (General Electric 10s 14 Batch NR), placed directly over each chamber. All other factors of the animal's environment were maintained as constant as possible. The water within the current chambers was not changed during the experiments, but was aerated continuously by means of a single airstone suspended a few centimeters above the substrate. The temperature of the water within the chambers increased gradually and evenly throughout each experiment, due to the presence of the observers in the darkroom and the heat given off by the motor driving the paddle systems. The initial temperatures were in the range from 26–28° C but over the three day period rose in each case by 2 or 3° C.

The postlarvae were subjected to a constant current velocity of 5.5 cm/sec, while the current velocity in the case of the juveniles was 7.5 cm/sec.

The shrimp were collected on appropriate tides from Buttonwood Canal within the Everglades National Park, Florida, using "Discovery" type plankton nets suspended into the current from a bridge over the canal. They were transported immediately to the laboratory, the journey taking approximately 2 hours and placed within the current chambers. In the postlarval experiment approximately 200 individuals were placed in each chamber; 10–12 individuals were used in the juvenile experiments.

Records of the movement of the shrimp within the chambers were initiated at midday on the day following collection and were continued for three days. In the case of the juveniles collected from a very early morning ebb tide, the experiments were initiated at midday of the day of capture. In all experiments the movements of the shrimp within the current chambers were recorded at half-hour intervals. They were recorded in terms of the number of shrimp swimming downstream and the number swimming upstream during a two-minute period.

The animals were not fed for the duration of the experiments, as feeding rhythms (Hughes, 1968) could have interfered with the rhythms under investigation.

Results

Postlarvae

The results (Fig. 1) show a pattern of up- and downstream swimming in the current chamber which is clearly in phase with the tide-cycle in nature. Upstream swimming in the chambers is greatest at times of flood tide in the area of capture, whereas downstream swimming predominates at times of ebb tide. The validity of these results is strongly supported by the marked similarity of the pattern obtained in both current chambers. It is further verified by results (not presented

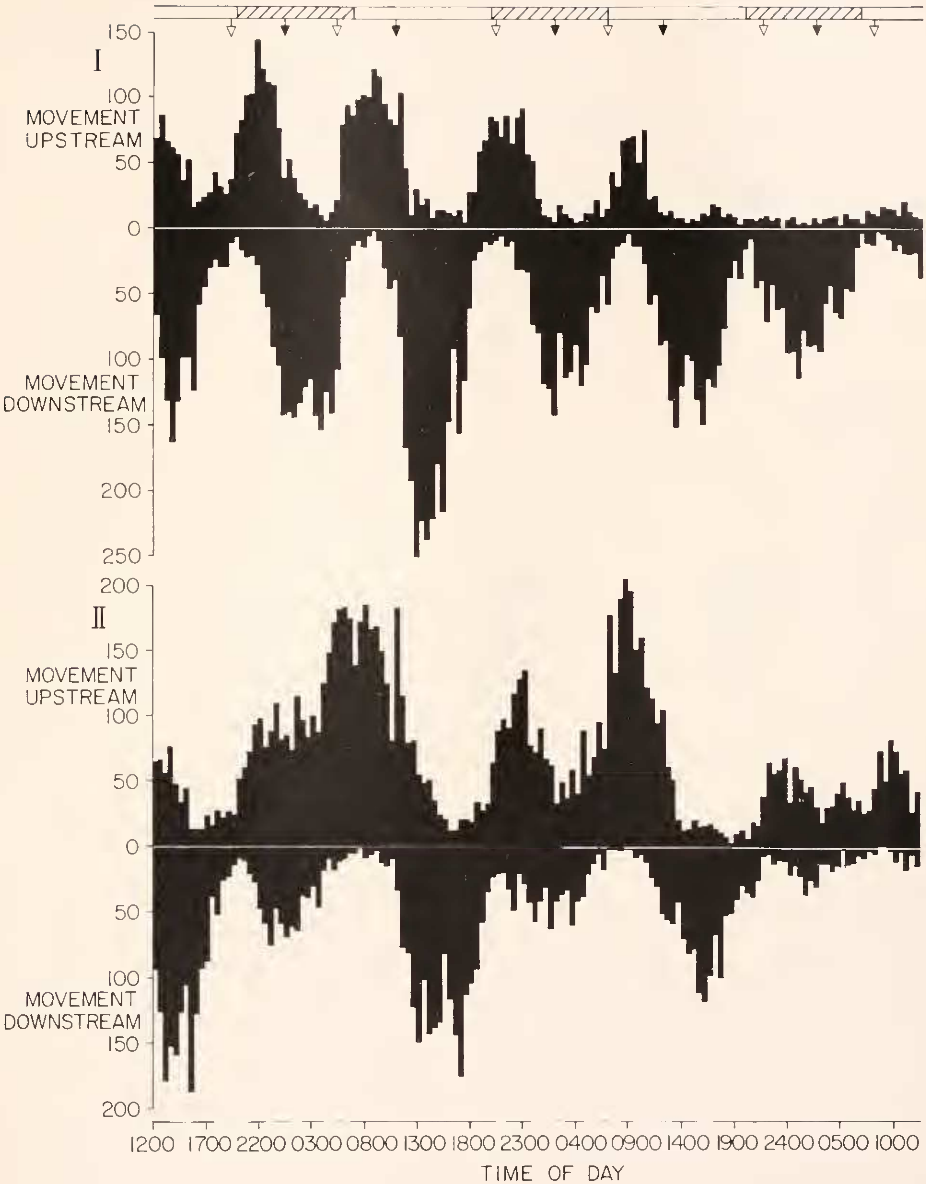

FIGURE 1. The pattern of swimming of postlarval shrimp maintained under constant conditions within two current chambers (I and II) for three days following their collection from nature. Swimming was recorded in terms of the numbers of individuals which moved in an up or downstream direction during two minute observation periods made at 30 minute intervals. The times of day and night in nature are represented by the open and transverse bars, respectively, at the top of the figure. Time of low and high tide in nature are indicated by the open and shaded arrows, respectively. (See text for description of constant conditions.)

here) of a preliminary experiment which had to be discontinued due to a malfunction within the current chamber system. Prior to discontinuation of that experiment, the animals showed peaks of up- and downstream swimming identical to those obtained in the experiments recorded here.

There is no indication from these results of circadian rhythmicity. The tendency to be active is apparently as great during the hours corresponding to "day" as during those corresponding to "night." The decrease in the level of activity which is evident by the third day is probably as much a function of starvation as a decline in the strength of the rhythm.

A high degree of endogenous control, in which the influence of both circadian and tidal rhythms may be discerned, is evident from these results (Figs 2 and 3). Endogenous control is evidenced by (i) the marked similarity of the direction and velocity of swimming of all individuals in the same tank (ii) the similarity of patterns of swimming obtained at all times in both tanks and (iii) the reproducibility of the pattern each day.

The nature of the relationship existing between the pattern of swimming and the tide regime from which the shrimp had been collected confirmed the results of previous experiments (Hughes, 1969b) in which it was found that shrimp, collected from an ebb tide occurring early in the evening (new and full moon), would, the following night in the current chamber, swim downstream for an interval which appeared to correspond to the duration of the ebb tide (Fig. 2). Thereafter they reversed direction and swam upstream for the remainder of the "night." The results of this most recent series of experiments show that this was not always the case but, by the time of the second and third "night," downstream swimming took place for a longer period and, sometimes extended even to the time of "dawn." Nevertheless, although it is not readily conveyed by the figures, it was usually apparent that the swimming behavior of the shrimp changed each night at about the time of the end of the ebb tide. Active downstream orientation diminished, often quite sharply, giving way to passive drifting and "indecisive" movements. Downstream displacement was scarcely diminished however, indicating that, although the juveniles actively orient in a downstream direction, like the postlarvae, they do not apparently swim very actively and their displacement downstream is largely a function of current velocity. Downstream swimming, which would be expected to occur during the subsequent early morning ebb tides, is absent, however, and only during the second "day" of Figure 2(II) is there the inactivity, characteristic of shrimp in nature (Fuss and Ogren, 1966), and which has been shown to occur in laboratory studies within stationary water under constant conditions (Hughes, 1968) and in current chambers when a day/night cycle is artificially imposed (Hughes 1969b).

The pattern of swimming of shrimp collected from an ebb tide occurring late in the evening (quarter moons) also confirmed earlier results (Hughes 1969b) insofar as, during the first night at least, the shrimp swam upstream throughout the night (Fig. 3). However, after the first night in the current chamber, these shrimp, when swimming, oriented almost exclusively downstream. The onset of the downstream swimming seemed to be determined by the time of the start of an ebb tide and was terminated the following day at apparently the time of dawn. Identical results (not presented here) were obtained when this experiment was repeated again with shrimp collected from a late evening ebb tide.

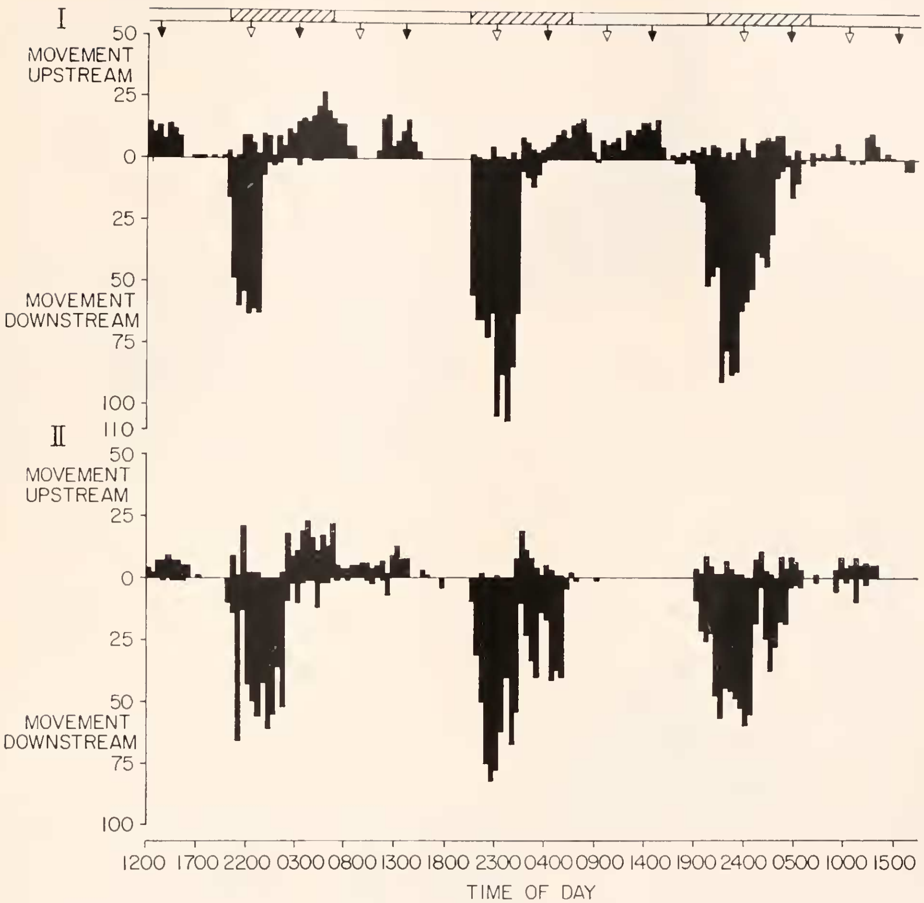

FIGURE 2. The pattern of swimming of juvenile shrimp collected from an early evening ebb tide (Full Moon). The shrimp were maintained under constant conditions within two current chambers (I and II) for three days following their collection from nature. Swimming was recorded in terms of the number of individuals swimming upstream and downstream during two minute observation periods made at 30 minute intervals. For further explanation see Figure 1.

In shrimp collected both from early and late ebb tides it appeared that upstream swimming, at what may be considered appropriate times, is only possible in recently collected animals. Those maintained in a current chamber for longer than a day or two often appear incapable of the "effort" involved and will frequently drift or swim downstream.

Discussion

Postlarvae

An endogenous tidal rhythm of swimming was shown in which upstream and downstream swimming were manifested at the times of flood and ebb tides,

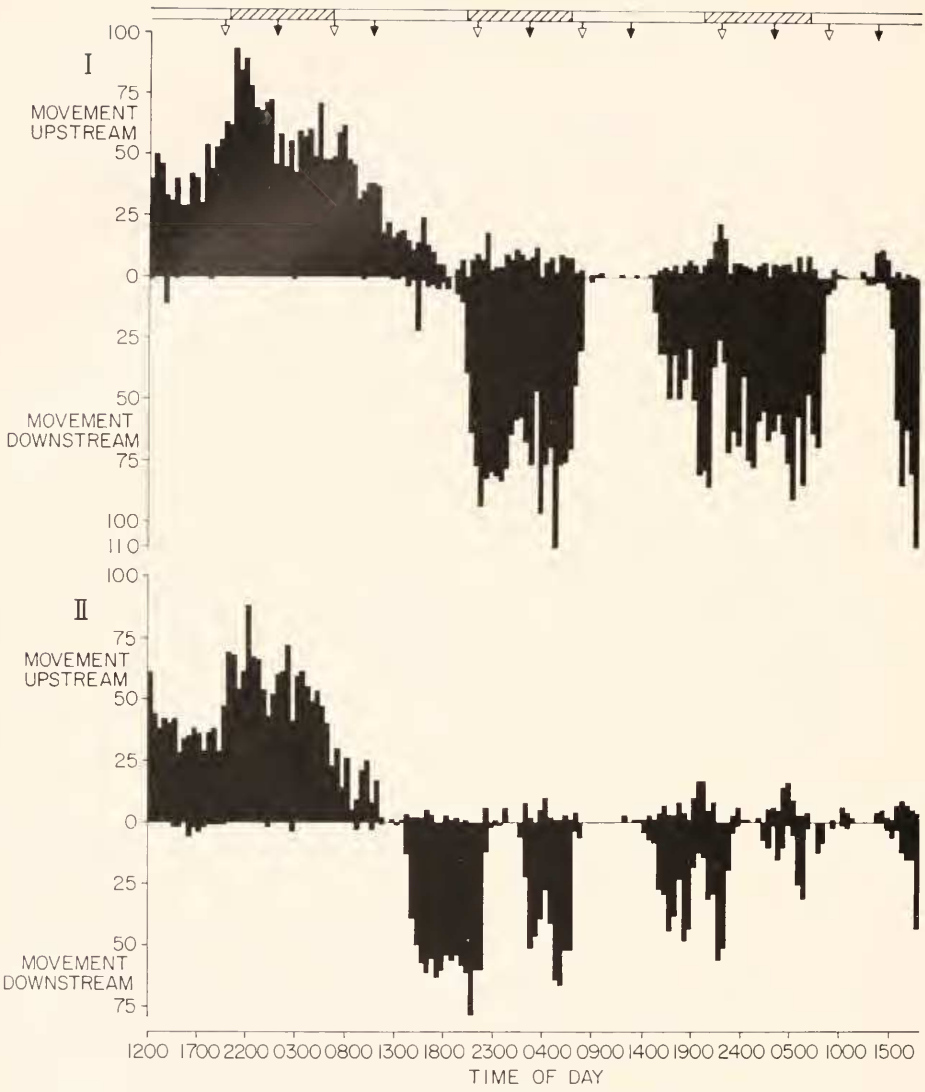

FIGURE 3. The pattern of swimming of juvenile shrimp collected from a late night ebb tide (Quarter Moon). For further explanation see Figure 1.

respectively, in the complete absence of externally changing environmental factors. The upstream and downstream phases which predominated at the times of alternate tides are not only phases during which shrimp swim in opposite directions with respect to the current but also differ with respect to the level of activity involved. The level of activity involved in downstream swimming, is considerably lower than that employed when swimming upstream. This is evident from the fact that counts, made during times of downstream swimming, were approximately of the same magnitude as those made during times of upstream swimming, whereas with the aid of the current, shrimp, actively swimming downstream, would be able to cover a far greater distance in unit time than those swimming against the same current.

The precise mechanism whereby these periods of up and downstream swimming, in phase with alternate tides, enable the postlarvae to utilize the tides for their displacements is not clear, but it is probable that during the active flood tide period the animals penetrate the water column above the substrate. In this position they are readily displaced in an inshore direction by the current. During the relatively inactive ebb tide period their movements may be confined to the substrate where, despite their downstream orientation, displacement by the current is minimal. This interpretation is in accord with the hypothesis previously expressed (Hughes, 1969a) to account for the mechanism whereby responses to salinity changes effect tide-associated displacements of postlarvae. Here it was thought that the increase in salinity, correlated with the flood tide, elicted activity within the water column, whereas the decrease of salinity at the time of ebb tide depressed activity and, with the marked reluctance of shrimp to move from water of higher to water of lower salinity, confined them to the substrate where they would more readily evade displacement by the current.

It is also evident that there is no essential difference between the orientation of postlarvae and juveniles with respect to currents at times of ebb and flood tide. Both appear to swim against flood tides and with ebb tides. The fact that they are displaced in opposite directions by the tides is explicable in terms of other aspects of their behavior which determines their presence or absence in the water column. High activity of postlarvae at times of flood tide leads them into the water column where they are readily displaced in an inshore direction. The active juveniles, however, remain in almost constant contact with the substrate orienting into and swimming strongly against the current, thereby resisting displacement.

Juveniles

In a previous publication (Hughes, 1969b) evidence was presented which indicated that swimming of migrating juvenile pink shrimp is under some measure of endogenous control. The observations reported in that publication were not carried out for longer than two days after collection of the animals, and the shrimp were exposed in the current chamber to a day-night cycle similar to that in nature. The light-off and light-on stimuli at the time of "sunset" and "sunrise," respectively, remained as effective cues for the phasing of swimming activity. On the other hand, the experiments reported here were run for three days under constant conditions in which the animals could, presumably, obtain no cues from their environment.

Although the results of the earlier experiments were confirmed and it has been clearly shown that swimming is under endogenous control there is nevertheless much about the form of the patterns obtained which is not clear. The pattern of swimming of shrimp collected at times of new and full moon (Fig. 2) still differed markedly from that of shrimp collected at the time of the quarter moons (Fig. 3) and only in the case of shrimp collected from ebb tides occurring early in the evening (full and new moons), is the adaptive phasing of the pattern of swimming with the natural tidal and diurnal cycle seemingly apparent.

The actual patterns obtained in the current chambers are probably a consequence of the interactions of oscillations of the tidal and circadian timing mechanisms. It may be that in the absence of appropriate environmental stimuli, the interaction of the two oscillating systems, tidal and circadian, gives rise to patterns of swimming activity which reflect the relative strengths of various Zeitgeber associated with the two systems. For example, in the case of shrimp collected from a late evening ebb tide (Fig. 3) it appears that periods of swimming were terminated at the time of dawn but were initiated, after the first night, at the time of the start of an afternoon ebb tide.

It is not evident why downstream swimming is manifested in the current chamber only by juveniles collected from ebb tides occurring in the early evening and, even then, only during the time of early evening ebb tides. Presumably endogenously induced downstream swimming at all night-time ebb tides would be more advantageous, and certainly more comprehensible in terms of the underlying rhythm involved.

Circadian rhythmicity in migrating postlarvae

It is well established that migrating postlarval pink shrimp may be collected from within the water column almost exclusively during the hours of darkness (Tabb *et al.*, 1962; Williams and Deubler, 1968; Roessler and Rehrer, in press). This relationship results apparently from a direct behavioral response of the postlarvae to light and there is, as indicated by these results, no endogenous component serving to confine activity to night. This contention is supported by the above mentioned workers who all record circumstances in which the behavior of postlarvae were influenced by prevailing light intensities. Tabb and his co-workers found that almost as many postlarvae were caught on a flood tide in the afternoon of a cloudy day as were caught after dark on the same day. Williams and Deubler on the other hand, found that a bright light at night, in the vicinity of their collecting station, drastically reduced their catch. In addition they found that higher catches were made at times of new moon than full moon. This was substantiated by Roessler and Rehrer who found that the postlarvae were closer to the substrate at full moon but more evenly distributed in the water column at times of new moon.

Circadian rhythmicity in migrating juveniles

These results are in accord with those of an earlier study (Hughes, 1968) in which it was found that the diurnal pattern of activity of juvenile shrimp greater than about 4 cm in total length was under a considerable measure of endogenous control, whereas shrimp smaller than this size exhibited an apparently greater responsiveness to exogenous stimuli and a lesser dependence on the endogenous rhythm. Unlike the results of this earlier study the results presented here do not show clear persistence of the diurnal pattern of activity and inactivity at night and by day respectively. It seems that the influence of the tidal cycle is manifest only when the shrimp are maintained with a current of water and not, as in the previous experiments, when maintained in aquarium tanks. In these experiments the interaction of this tidal rhythm with the circadian apparently obscures the clear manifestation of either. However, the circadian rhythm, which undoubtedly contributes to maintaining the diurnal periodicity of activity, is evident. Its influence is exhibited by virtue of the fact that times of inactivity occur only during the time of day. Circadian rhythmicity is further evident in the case of the juveniles collected from an early evening ebb tide (Fig. 2) the periods of downstream swimming are initiated each day at the time of sunset while in the case of those collected from late night ebb tides (Fig. 3) downstream swimming is terminated each day at the time of sunrise.

Adaptive significance of endogenous control

The efficacy of tide-associated displacements as a mechanism to enable movements into or out of inshore waters is probably greatly enhanced by the endogenous phasing of adaptively appropriate behavior with the prevailing tide cycle.

Direct response to the water quality (or other factors indicating change of tide) would not, for several reasons, be as effective a mechanism as one in which this direct response is further controlled endogenously. The most obvious problem overcome through endogenous control is one which was raised by Creutzberg (1961) in his study of tide-associated displacements of elvers. He found it difficult to explain the mechanism whereby elvers which, during the flood tide, had risen to higher levels within the water column, would be able to perceive the end of the flood if they remained in that same water mass. This is a problem which would similarly face pink shrimp and all other organisms utilizing tides for their displacements. These results suggest that, in pink shrimp post-larvae the duration of the active and inactive periods coinciding with flood and ebb tides respectively is endogenously limited, affording them a degree of independence from water quality cues. The latter will still serve to maintain the phase relationship between times of activity/inactivity and the flood/ebb cycle.

In the case of the juveniles there is less evidence from these results that the endogenous tidal rhythm manifests itself overtly in adaptively advantageous behavior. The downstream swimming evidenced at the time of an early evening ebb tide by individuals collected the previous night from an early ebb tide (Fig. 2) and its subsequent reversal to upstream swimming at about the time of change of tide, is the only clear suggestion of an adaptive association existing between tides and behavior. It is probable, however, that a changing responsiveness to decreasing or increasing salinity, or whatever other stimulus denotes tidal change, exists and that at times of change of tide the animal is maximally responsive to the appropriate stimulus and maximally "geared" to carry out appropriately adaptive behavior for an interval equivalent to the duration of the tide.

I gratefully acknowledge the financial support given to me by the National Geographic Society. Further support was obtained from the National Science Foundation, Sea Grant Award, Nos, GH-58 and GH-100, to the University of Miami.

Considerable help in the conduct of the experiments was given by Dorothea Wiedemann and Alan Dunlap.

Summary

1. Swimming of both postlarval and juvenile pink shrimp was recorded in current chambers in the laboratory for three days following collection from nature.

2. In the apparent absence of environmental cues the animals maintained various forms of phase relationship with the tidal and diurnal cycles.

3. Postlarvae manifested a pattern of swimming, markedly in phase with the semi-diurnal tide cycle. Upstream swimming took place during flood tides and downstream swimming during ebb tides. No circadian periodicity was found and the confining of their activity in nature to night-time is considered a direct response to prevailing light intensity.

4. The patterns of swimming evidenced by juveniles differ depending, apparently, on some as yet undetermined aspect of the tide cycle to which they are exposed prior to collection. Individuals collected at times of new and full moon, when ebb tides occur early in the evening, exhibit a different pattern of swimming from those of individuals collected at times of quarter moons when ebb tides occur late at night. The patterns obtained are clearly endogenous although their adaptive phasing with the tidal and diurnal cycles is not always evident.

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